

GENETIC DIFFERENTIATION OF LIFE HISTORY TRAITS IN POPULATIONS OF *MESOCYCLOPS EDAX* (CRUSTACEA: COPEPODA)

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ABSTRACT

Differences in maturation time, body size and clutch size among populations of the freshwater copepod *Mesocyclops edax* inhabiting lakes of different seasonalities (Lake Thonotosassa, Florida, and Douglas Lake, Michigan) were maintained through two generations under common laboratory conditions. In most cases, Florida individuals matured more rapidly and had larger body sizes and clutch sizes than Michigan individuals over a range of temperature from 15 to 30°C. The greatly reduced fecundity and longer maturation time of the Michigan population relative to the Florida population at 15°C may reflect adaptations to different temperature regimes encountered by these geographically distant populations. Genotype-environment interactions were observed for body size, but not for maturation time or clutch size. Some local variation was evident in both the Michigan and Florida locales, indicating that forces operating on a local scale may result in substantial variation that is superimposed upon any broad scale, geographic patterns.

Selection for short maturation time and large clutch size is hypothesized to have occurred in the Thonotosassa population, which is exposed to heavy fish predation and high food levels. The small bodies and clutches in the Douglas population, which experiences chronically low food levels, may reflect selection to minimize energy demands where food is scarce.

INTRODUCTION

An underlying assumption pervading much of life history theory is that at least part of the variation observed within and among populations is genetically based and represents local adaptation to specific environments. The recent growing interest in integrating ecological and genetical approaches to understand life history evolution emphasizes the fundamental need for establishing the heritable basis of such variation when investigating its adaptive significance (Dingle and Hegmann, 1982; Lande, 1982). When such experiments are conducted over a range of environments, the genetic expression of life history traits sometimes can be observed to vary according to the environment in which it is measured (Clausen *et al.*, 1948; Berven 1982a, b). Changes in relative performances across environments may alter conclusions derived from experiments conducted in just one environment, as well as provide insight into how organisms may adapt to entire environmental regimes.

The present study was designed to determine whether populations of the widely distributed freshwater zooplankter *Mesocyclops edax* (Crustacea:Copepoda) differ genetically with respect to life history traits. The isolated water bodies inhabited by freshwater copepods may reduce gene flow among populations, thereby increasing the likelihood of adaptation to specific environments. Populations inhabiting environments that differ with respect to physical and biological factors and are widely separated

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geographically (Florida, Michigan), were chosen to increase the probability of finding genetic differences. The life history traits examined were maturation time, adult body size, and clutch size. The responses of these traits over a temperature range of 15 to 30°C were examined to ascertain the presence of any genotype–environment interaction. Temperature is a well documented influence on the phenotypic expression of life history traits in copepods (Coker, 1933; McLaren, 1965; Burgis, 1970; Herzig, 1983), but studies that directly examine the heritable basis of such phenotypic responses to temperature are few (Battaglia, 1959; McLaren, 1976; Bradley, 1978a). In addition to temperature, food level in the study lakes is compared and its potential role as a selective force is discussed. Two populations were examined from each locale to compare the extent of local variation with large scale geographic variation.

MATERIALS AND METHODS

Study sites

The primary experimental populations were collected from Douglas Lake in Cheboygan Co., Michigan, and Lake Thonotosassa in Hillsborough Co., Florida. One additional lake (Fairy Lake, Florida, and Lake Cochran, Michigan), each located within 35 km from the main study lake, was selected in each of the two counties to examine local variation within Michigan and Florida. Trophic classifications were based on Secchi disc transparency and chlorophyll *a* measurements and assigned to the Michigan lakes according to Carlson's (1977) trophic state index, and to the Florida lakes according to the interpretation of Carlson's index for Florida lakes by Beaver and Crisman (1982). Lake Thonotosassa is eutrophic-hypereutrophic (Cowell *et al.*, 1975; Wyngaard *et al.*, 1982) and Douglas Lake is mesotrophic-eutrophic and is described by Welch (1927), Tucker (1957) and Lind (1978). Fairy Lake, Florida, is in the upper portion of the range of trophic state indices for oligotrophic lakes (Young, 1978; Elmore, 1983) and Lake Cochran, Michigan, is mesotrophic (Gannon and Paddock, 1974; Fairchild, 1980). Lake Thonotosassa contains the highest planktivorous fish densities (Langford, 1975), followed by Douglas Lake (Smith, unpub. data), which has a diverse fish assemblage. Densities of planktivores (vertebrate and invertebrate) are low in Lake Cochran (Fairchild, 1980) and Fairy Lake (Young, 1978; Elmore, 1983). Throughout this paper individuals from Lake Thonotosassa, Fairy Lake, Lake Cochran, and Douglas Lake are referred to as FT, FF, MC, and MD individuals, respectively.

Field measurements

Copepods were collected with a No. 20 net (76 μm), narcotized with CO₂ and preserved in 4% formaldehyde before measuring body size. Female body size and clutch size of MD and FT individuals were measured several times during the year to span a range of temperatures. Egg volumes were measured using MD and FT individuals collected during early summer. Egg volume was determined by measuring five eggs from each clutch, and calculated using the volume of a prolate spheroid = $\frac{4}{3} r_1 r_2^2$, where r_1 is the long axis and r_2 is the short axis. Male body size of MD and FT individuals was measured using collections from May and September, respectively, to obtain males that matured at comparable temperatures. Cephalothorax length was measured at 40 \times with a compound microscope. Body size and clutch size of MD and FT females were compared using samples collected during several seasons. Body size and clutch size of FF individuals were determined from a spring and summer collection and those of the MC population from a summer collection.

Chlorophyll *a* concentrations, used as a measure of food level, were determined

from samples collected bi-weekly from Douglas Lake from June through October, 1980 in the deepest portion of South Fishtail Bay and weekly measurements at the surface, 5 m, 10 m, 15 m, and 17 m from 3 July to 28 July (Evans and Glover, unpub. data) also were available. Chlorophyll samples from Lake Cochran were collected at monthly intervals at 1.5 m from June–September, 1980, in the deepest portion of the lake. The procedures used to measure chlorophyll *a* content of water samples from the Michigan lakes were the same as those used to analyze the Florida water samples (Wyngaard *et al.*, 1982; Elmore, 1980), except that a Turner Fluorometer III was used in the former analyses.

Laboratory rearing

The life cycle of *M. edax* consists of an embryonic (egg) stage, six larval (nauplius) stages, five juvenile (copepodid) stages, and an adult stage which does not molt. Michigan populations show a facultative diapause from late fall to early spring. From spring to fall the Michigan populations complete two generations without any diapause. In the Florida population development from egg to adult proceeds continuously throughout the year. The typical diet during the early stages consists of algae, protozoans, and bacteria and diversifies to include larger animals (rotifers, cladocerans, copepods) in the later stages.

For the laboratory rearing studies ovigerous females were collected from the field and their eggs allowed to hatch under the experimental conditions. The only exceptions to this were the 25°C life tables of FT and MD populations for which virgin females were mated in the laboratory. Animals were reared individually in the laboratory for two generations under constant, defined conditions to ensure that all populations were reared in a common environment and that conditions were repeatable over time. Experiments were generally initiated when the lake temperature approximated the laboratory temperature (Table I). MD and FT copepods were reared at 15 ± 0.5°C, 25 ± 0.5°C and 30 ± 0.5°C to determine expression of life history traits at each of three temperatures. FF and MC individuals were reared at 25 ± 0.5°C for examination of local variation. All collections of Michigan animals were made in early summer to ensure that laboratory generations one and two paralleled those in the field and did not overlap with the period when animals normally were in diapause.

TABLE I

Collection dates and lake temperatures of laboratory reared populations of Mesocyclops edax

Population	Date collected	Lake temperature °C	Laboratory temperature °C
Michigan			
Douglas	June 1982	21	15
Douglas	June 1981	22	25
Douglas	June 1982	21	30
Cochran	June 1982	22	25
Florida			
Thonotosassa †	February 1980	12.8	15
Thonotosassa	July 1981	31.0	25
Thonotosassa	August 1982 (rep 1)	28.8	30
	June 1982 (rep 2)	28.0	25
Fairy	April 1982 (rep 1)	24.4	25
	September 1982 (rep 2)	29.5	25

Life tables of the FT individuals reared at 30°C and FF individuals reared at 25°C were replicated with samples collected during different seasons in order to reveal genetically based seasonal variation that may have existed within a population (Table I).

Upon hatching, nauplii were transferred to a petri dish 20 mm in depth and 60 mm in diameter containing 15 ml of artificial lake water and 10^4 cells/ml of the flagellated yellow-brown alga *Cryptomonas ozolini* Sküjja. Individuals were transferred by a wide pipette every other day to a clean dish containing fresh medium and algae. Handling mortality was clearly negligible, as survival at 25°C was 97%. Food densities did not decrease below 10^4 cells/ml on the second day. Upon reaching maturity, adults were fed three juveniles (copepodid stages I–III) of the calanoid copepod *Diaptomus dorsalis* (Marsh) daily. The light:dark cycle for all organisms reared in this study was 14:10.

C. ozolini was isolated from Douglas Lake by D. Fuller and can be obtained from the Starr Collection at the University of Texas at Austin (culture number UTEX-LB2194). Formulae for the artificial lake water and algal media and details of culture methods of alga and *Diaptomus* (from Lake Thonotosassa) are given in Wyngaard and Chinnappa (1982).

Because of very low reproduction of the MD population at 15°C, only one generation was reared at this temperature. The trends in statistically significant differences between the FT, FF, and MC populations were similar for both generations (Wyngaard, 1983); thus the analyses of the four populations presented in this paper were based upon the first generation only.

Statistical procedures

Statistical tests used in this study included *t*-tests and 2×2 tests of independence (*G*-statistic) (Sokal and Rohlf, 1969). Statistical significance is taken to be .05 or less. The experimental design for examining genotype-environment interactions yielded unbalanced data sets, which were analyzed using the GLM procedure of S.A.S. (Helwig and Council, 1979). Sample sizes used in the analyses for any one trait ranged from 474–707 individuals. As some individuals were related (*i.e.*, brothers or sisters of same brood), the ANOVA were performed on family means that were weighted by family size, yielding 93–225 observations. Family size ranged from one to ten individuals. Least squares means were calculated for all laboratory reared animals in this study, so that large and small families would be weighted accordingly. One trait, maturation time, was transformed to natural logarithms. The assumption of homogeneity of variances among treatments was satisfied in all tests.

RESULTS

Field analyses

Field collections revealed differences between the MD and FT populations in most traits examined (Table II). Similar trends between populations in female body size and clutch size occurred regardless of season, with the exception of FT females collected in winter which were smaller than MD females collected during spring and summer (Appendix). Thus samples collected during several seasons over a year were lumped in the comparisons. FT females were significantly larger and had larger clutches, but significantly smaller eggs than MD females (Table II). FT males were larger than MD males. The coefficients of variation for specific traits were similar between populations,

TABLE II

Means (\bar{X}) and coefficients of variation (C.V.) of traits of field caught *Mesocyclops edax* from Douglas Lake and Lake Cochran, Michigan, and Lake Thonotosassa and Fairy Lake, Florida

Trait	Michigan		Florida		<i>P</i> (MD vs. FT)				
	Douglas	Cochran	Thonotosassa	Fairy					
	\bar{X}	(C.V.)	\bar{X}	(C.V.)					
Female body size (μm)	696.0 n = 138	(9.5)	718.1 n = 89	(7.0)	761.9 n = 164	(6.8)	758.3 n = 126	(6.3)	<i>P</i> < .001
Male body size (μm)	416.2 n = 50	(3.8)			491.0 n = 52	(4.7)			<i>P</i> < .001
Clutch size	20.4 n = 50	(16.1)	22.4 n = 20	(14.1)	51.2 n = 154	(29.2)	33.5 n = 34	(23.9)	<i>P</i> < .001
Egg volume ($\text{mm}^3 \times 10^{-3}$)	0.571 n = 70	(23.3)			0.239 n = 70	(32.2)			<i>P</i> < .001

Numbers of individuals are indicated by n. Means of populations are compared using *t*-tests.

with the exception of clutch size which was markedly less variable in the MD population (16.1%) than in the FT population (29.2%).

Samples of Michigan copepods collected in June most likely contained individuals that experienced comparable temperatures throughout their lifetime, as they in all likelihood hatched from eggs produced by the previous diapausing generation and were used to compare field collected MD and MC individuals. MD females (737.8 μm) were larger than MC females (718.1 μm) ($t(144 \text{ df}) = 2.2$, $P < .01$), but mean clutch size of MD females (20.06) was smaller ($t(49 \text{ df}) = 24$, $P < .05$) than MC females (22.45). Female sizes were not significantly different between FT and FF populations averaged over the year, but FT females had larger clutches than FF females ($t(186 \text{ df}) = 9.68$, $P < .001$) (Table II). Clearly individuals from lakes within a locale were more similar than those between Michigan and Florida.

Laboratory analyses

Maturation time. FT females and males matured significantly more rapidly than MD individuals when reared in a common laboratory environment at 15, 25, and 30°C, except for males which did not differ significantly at 30°C (Fig. 1). Females and males showed similar responses over the temperature range as evidenced by the lack of a population-environment interaction.

Local variation was evident at both locales (Table IV). MD females matured significantly more rapidly (15.8 days) than did MC females (20.6 days). Both FT females and males matured more rapidly than FF females and males, respectively.

Body size. FT females and males had larger body sizes than MD females and males, respectively, at 15 and 25°C (Fig. 2). FT and MD females did not differ significantly at 30°C but MD males were significantly larger than FT males. Generation two FT and MD males were used in the comparison at 25°C because many MD males of generation one at this temperature were eaten by females following mating, and could not be measured. This predation may have resulted in a biased sample of males available for measurement, and could explain why mean body size of generation one

TABLE III

ANOVA of maturation time in two populations (Douglas and Thonotosassa) of *Mesocyclops edax* in three environments (15, 25, and 30°C)

Females				
Source	d.f.	M.S.	F	P
Population	1	0.727	23.6	<.001
Environment	2	33.954	1103.9	<.001
Population × environment	2	0.016	0.5	N.S.
Error	220	0.031		
Total	225			
Males				
Source	d.f.	M.S.	F	P
Population	1	0.251	10.6	<.001
Environment	2	31.558	330.7	<.001
Population × environment	2	0.052	2.2	N.S.
Error	186	0.024		
Total	191			

FT males (466.3 μm) reared at 25°C was less than the mean body size of MD males (482.7 μm) (Wyngaard, 1983b). For this reason when rearing generation two at 25°C, randomly selected groups of FT and MD males were not mated but instead preserved upon reaching maturity. Generation two FT males reared at 25°C were significantly larger than generation two MD males ($t(136 \text{ df}) = 3.95, P < .001$) (Fig. 2). These latter results more likely reflect the true comparison of male body size of the FT and MD populations. Difference in body size was not evident between populations at the

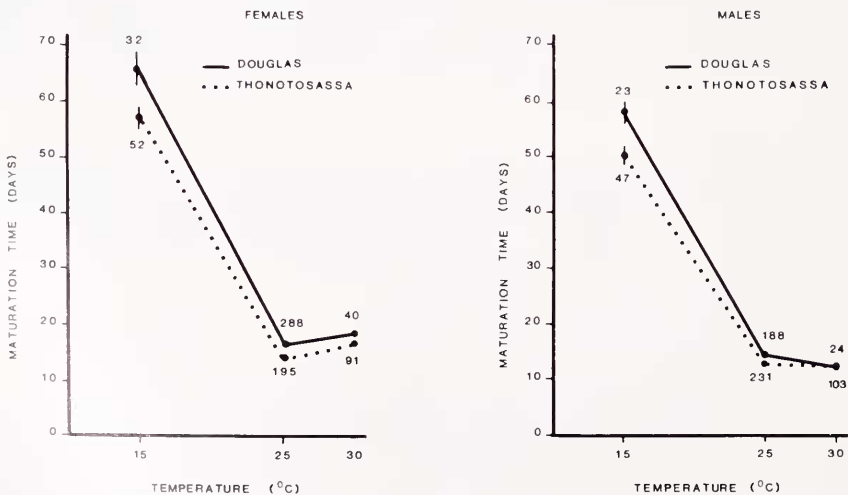


FIGURE 1. Mean maturation time of female and male *Mesocyclops edax* at three temperatures from Douglas Lake, Michigan (—) and Lake Thonotosassa, Florida (---). Numbers and vertical lines refer to number of individuals and one standard error, respectively. Error bars at 25 to 30°C are contained within the dot.

TABLE IV
Least squares means (\bar{X}) and standard errors (S.E.) of life history traits of generation one Lake Thonotosassa and Fairy Lake, Florida, and Douglas Lake and Lake Cochran, Michigan, individuals reared at 25°C

	Florida				Michigan				
	Thonotosassa		Fairy		Douglas		Cochran		
	\bar{X}	(S.E.)	\bar{X}	(S.E.)	\bar{X}	(S.E.)	\bar{X}	(S.E.)	
Females									
Maturation time (days)	14.0	(+0.39) (-0.38) n = 195	18.1	(+0.05) (-0.05) n = 71	15.7	(+0.39) (-0.38) n = 188	20.5	(+0.47) (-0.46) n = 62	<.001
Body size (μ m)	699.3	(6.17) n = 144	649.3	(7.31) n = 63	663.3	(5.16) n = 226	679.2	(7.68) n = 45	N.S.
Clutch size	35.51	(0.93) n = 59	24.20	(0.79) n = 30	21.95	(0.82) n = 70	19.90	(1.03) n = 19	N.S.
Males									
Maturation time (days)	12.5	(+0.32) (-0.30) n = 231	14.0	(+0.29) (-0.28) n = 52	13.6	(+0.35) (-0.34) n = 188	14.2	(+0.25) (-0.25) n = 63	N.S.
Body size (μ m)	499.6	(4.26) n = 92	475.1	(4.95) n = 29	482.7	(5.06) n = 36	491.2	(3.70) n = 59	N.S.
Survival	96.77		84.82		97.16		76.68		<.001

Geometric means and 95% confidence intervals of maturation time are presented, as these data were log transformed in the statistical analyses. Numbers of individuals are indicated by n. Probability limits are for comparisons between populations within each locale.

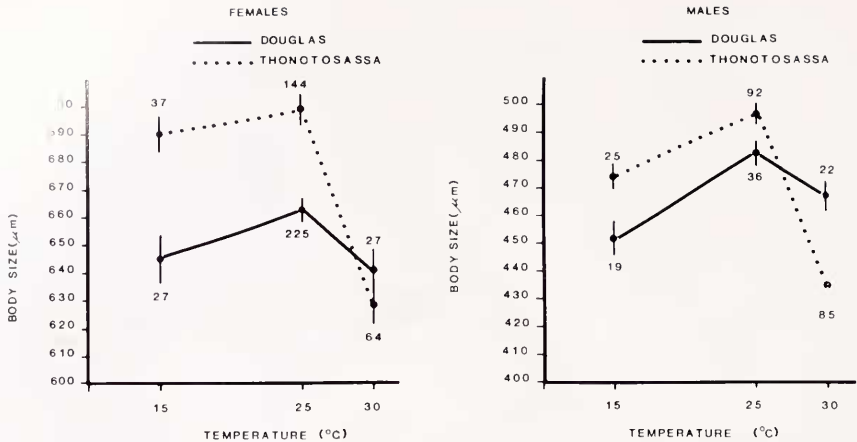


FIGURE 2. Mean body size of female and male *Mesocyclops edax* at three temperatures from Douglas Lake, Michigan (—) and Lake Thonotosassa, Florida (---). Numbers and vertical lines refer to number of individuals and one standard error, respectively.

Michigan locale, but FT females and males were larger than FF females and males, respectively (Table IV).

Female and male body sizes were the only traits in this study that exhibited a significant genotype-environment interaction, as examined by two-way ANOVA ($F_{2,189} = 10.09$, $P < .001$ for females; $F_{2,135} = 15.00$, $P < .001$ for males) (Table V) and response curves (Fig. 2). Males were significantly smaller at 15°C than at 25°C in both MD ($t(53 \text{ df}) = 3.70$, $P < .001$) and FT ($t(115 \text{ df}) = 3.96$, $P < .001$) populations.

Clutch size. FT individuals had larger clutch sizes than MD individuals at 15, 25, and 30°C (Fig. 3). Only one MD female of generation one produced a clutch at 15°C. This clutch had 19 eggs, which is typical for this population at all temperatures in the

TABLE V

ANOVA of adult body (μm) size in two populations (Douglas and Thonotosassa) of *Mesocyclops edax* in three environments (15, 25 and 30°C)

Females					
Source	d.f.	M.S.	F	P	
Population	1	2343000	17.6	<.001	
Environment	2	3937000	29.5	<.001	
Population \times environment	2	1344000	10.1	<.001	
Error	189	133000			
Total	194				
Males					
Source	d.f.	M.S.	F	P	
Population	1	220000	4.9	<.05	
Environment	2	613000	13.5	<.001	
Population \times environment	2	680000	15.0	<.001	
Error	135	45000			
Total	140				

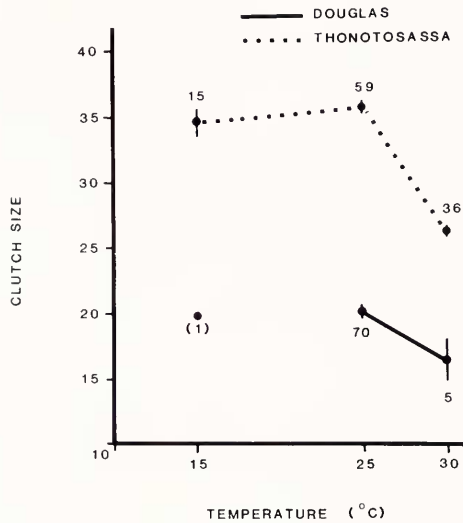


FIGURE 3. Mean clutch size of female *Mesocyclops edax* at three temperatures from Douglas Lake, Michigan (—) and Lake Thonotosassa, Florida (····). Numbers and vertical lines refer to number of individuals and one standard error, respectively.

field and lies outside the 95% confidence limits for the average clutch size (35.5) in the FT population at 15°C. Of the females offered males for mating, only one of 18 (5%) MD females and 15 of 48 (31%) FT females produced clutches. FT females had larger clutches than FF females, whereas clutch size was not significantly different between populations at the Michigan locale (Table IV).

Survival. Survival from hatching to adult varied considerably across temperatures. Both MD and FT individuals had highest survival (97.2%, 96.7%, respectively) at 25°C, and moderate survival (51.6%, 52.6%, respectively) at 30°C. A statistically significant difference in survival between these two populations was evident only at 15°C, at which FT individuals survived almost twice as well (64.7%) as MD individuals (36.7%) ($G(1 \text{ df}) = 24.14, P < .005$). Survival was significantly higher (97.2%) in the MD population than in the MC population (76.7%) and significantly higher in the FT population (96.8%) than the FF population (84.8%). Survival of FF and MC individuals was not significantly different.

Seasonal variation and acclimation. Additional life tables compared copepods from FT and FF populations collected at different seasons and reared through two generations in the laboratory. These studies revealed that the genetically based seasonal variation

TABLE VI

ANOVA of clutch size in two populations (Douglas and Thonotosassa) of *Mesocyclops edax* in two environments (25 and 30°C)

Females				
Source	d.f.	M.S.	F	P
Population	1	1766	101.8	<.001
Environment	1	677	39.0	<.001
Population × environment	1	53	3.1	N.S.
Error	90	17		
Total	93			

was minimal and did not alter the trends reported above. Mean values for FT individuals at 30°C reared from June and August collections were similar (Table VII), as were those of FF individuals reared at 25°C from May and September collections (Table VIII). In the instances in which statistically significant differences in mean values between replicate life tables exist, the differences between either replicate and the MD or FT population was in the same direction as reported in the above analyses. For example, comparison of FT individuals reared at 30°C from either the June or September collections to MD individuals reared at 30°C revealed the same trends in statistically significant differences. The only exception was a nonsignificant difference in female maturation time between MD and FT females collected in June. However, maturation time was not significantly different between the FT females reared from the September and June collections.

The sample sizes for generation one were larger than those of generation two in most cases, but the trends in statistically significant differences in life history traits between the MD *versus* MC and MD *versus* FT populations were the same for both generations (Wyngaard 1983). Exceptions to this occurred at 25°C at which generation one MD males were larger than FT males (see above) and at 30°C at which generation two FT males matured significantly faster than MD males.

The rearings of all FF populations were notable in that sex ratios were strongly biased toward females. This sex bias in the generation two FF population resulted in such a small number of males that it is difficult to ascribe any trends to certain traits

TABLE VII

Least squares means (\bar{X}) and standard errors (S.E.) of generation one individuals reared at 30°C in 1982 from June and August collections from Lake Thonotosassa, Florida, and a June collection from Douglas Lake, Michigan

	Douglas June		Thonotosassa June		Thonotosassa August	
	\bar{X}	(S.E.)	\bar{X}	(S.E.)	\bar{X}	(S.E.)
Females						
Maturation time	17.3	(+0.55) (-0.54)	16.6	(+0.49) (-0.47)	15.8	(+0.38) (-0.37)
	n = 40		n = 50		n = 91	
Body size (μm)	640.1	(7.61)	612.1	(5.63)	628.7	(5.44)
	n = 27		n = 37		n = 64	
Clutch size	16.80	(2.18)	24.9	(2.42)	26.4	(0.93)
	n = 5		n = 9		n = 38	
		<i>P</i> < .01			<i>P</i> < .05	
		<i>P</i> < .001			N.S.	
Males						
Maturation time	12.4	(+0.48) (-0.45)	13.18	(+0.36) (-0.36)	12.2	(+0.26) (-0.25)
	n = 24		n = 48		n = 103	
Body size (μm)	467.1	(5.32)	425.1	(5.22)	435.3	(3.01)
	n = 22		n = 20		n = 85	
		<i>P</i> < .001			<i>P</i> < .05	
% Survival	51.61		50.00		52.57	
		N.S.			N.S.	

Geometric means and 95% confidence intervals of maturation time are presented, as these data were log transformed in the statistical analyses. Number of individuals is indicated by n. Means of populations are compared using *t*-tests.

TABLE VIII

Least squares means (\bar{X}) and standard errors (S.E.) of generation one individuals reared at 25°C from collections in May and September of 1982 from Fairy Lake, Florida, and summer of 1981 from Lake Thonotosassa, Florida

Trait	Thonotosassa July		Fairy September		Fairy May	
	\bar{X}	(S.E.)	\bar{X}	(S.E.)	\bar{X}	(S.E.)
Females						
Maturation time	14.0	(+0.39) (-0.38)	22.9	(+0.80) (-0.77)	18.1	(+0.05) (-0.06)
	n = 195		n = 59		n = 71	
		$P < .001$		$P < .001$		
Body size (μm)	699.3	(6.17)	630.4	(5.93)	649.3	(7.31)
	n = 59		n = 46		n = 63	
		$P < .001$		$P < .05$		
Clutch size	35.51	(0.93)	24.25	(1.84)	24.20	(0.79)
	n = 59		n = 4		n = 30	
		$P < .001$		N.S.		
Males						
Maturation time	12.5	(+0.32) (-0.30)	20.1	(+1.43) (-1.12)	14.0	(+0.29) (-0.28)
	n = 231		n = 14		n = 52	
		$P < .001$		$P < .001$		
Body size (μm)	499.6	(4.26)	439.1	(5.86)	475.1	(4.95)
	n = 92		n = 12		n = 29	
		$P < .001$		$P < .001$		
% Survival	96.77		51.02		84.82	
		$P < .001$		$P < .001$		

Geometric means and 95% confidence intervals of maturation time are presented as these data were log transformed in the statistical analyses. Numbers of individuals are indicated by n. Means of populations are compared using *t*-tests.

with statistical confidence. Nevertheless generation one individuals did not show more statistically significant differences in traits among the four populations than generation two individuals, indicating that acclimation effects were minimal.

Summary. In most cases FT individuals matured significantly more rapidly, and had larger body sizes and clutch sizes than MD individuals when reared in a common laboratory environment at 15, 25, and 30°C (Figs. 1–3). Only female and male sizes exhibited a genotype-environment interaction. Local variation was evident in some life history traits at both the Michigan and Florida locales, but was greater at the Florida locale (Table V). These trends between populations did not change over the seasons (Tables VII, VIII).

Trophic characteristics of lakes

The four study lakes can be assigned to low or high food level, as measured by chlorophyll *a* content and algal cell volume (Table IX). Lake Thonotosassa exhibited by far the highest values; Douglas Lake, Lake Cochran, and Fairy Lake values were somewhat lower.

DISCUSSION

This study documents genetic differentiation with respect to several life history traits in geographically distinct as well as in local populations of the copepod *Mesocyclops edax*. The Michigan and Florida populations differed in all life history traits

TABLE IX

Cherax edax of the Michigan and Florida study lakes that reflect food level

	Florida		Michigan	
	Fairy	Thonotosassa	Douglas	Cochran
algal cell volume ($\mu\text{l/l}$)	3.9 ^a	11.9 ^a	3.5 ^a	—
chlorophyll <i>a</i> ($\mu\text{l/l}$)	10.9 ^a	91.6 ^a	6.0 ^{d,c}	3.0 ^{b,f}
(range)	(1.9–31.6) ^{a,c,f}	(26.0–110.4) ^{a,c,e}	(1.5–14.5) ^{b,d,f}	(0.8–11.0) ^{b,f}
percent blue green algae	18 ^a	68 ^a	80 ^b	—
percent green algae	78 ^a	26 ^a	3 ^b	—

^a Dawes and Cowell (1984).^b Fairchild (1980).^c Elmore (1983).^d Evans and Glover (unpub. data).^e Wyngaard *et al.* (1982).^f Wyngaard (unpub. data).

examined. FT individuals in most cases had the largest adult body and clutch sizes coupled with the most rapid maturation. MD and MC individuals were smaller, had smaller clutches, and slower maturation, whereas FF individuals were roughly intermediate between the Michigan populations and their FT counterparts. The genetically based differences in maturation time, body size, and clutch size among populations of *M. edax* suggest these populations have travelled separate evolutionary paths during the recent past. Additional genetical studies at another level support this view; the additive genetic variances in maturation time, body size, and clutch size also differ between the Michigan and Florida populations (Wyngaard, 1986). This species is one of the most widely distributed freshwater cyclopoids in North America, lives in water bodies of various sizes, trophy, pH, and community composition, and exhibits considerable phenotypic variation among populations (Forbes, 1897; Coker, 1943; Wilson and Yeatman, 1959; Wyngaard and Chinnappa, 1982). The present study clearly reveals that some of this phenotypic variation is genetically, rather than environmentally based. It is still premature, however, to conclude whether these differences reflect large scale geographic patterns or only local variation.

The relative magnitude of local compared to large scale geographic variation may depend, in part, upon barriers to gene flow. Strong genetic differentiation in the face of high levels of gene flow has been documented (Jain and Bradshaw, 1966; Antonovics and Bradshaw, 1970; Endler, 1973; McNeilly, 1968). Allan (1984), however, found no evidence of reproductive isolation between the MD and FT populations.

Possible explanations for genetic differences observed in the present study are founder effect, random drift, and different selective regimes. The wide geographical distribution and characteristically large population sizes of *M. edax* suggest that the first two explanations are not probable causes of the observed genetic differentiation. Studies of rates of gene flow, however, are necessary to rule out these two explanations.

The role of selection in molding the observed life histories is a logical consideration as these populations have presumably evolved in lakes that differ in temperature regime, resource availability, and predator level. Numerous ecological studies have implicated these factors as ones influencing population dynamics and phenotypic differences in life histories (review in Kerfoot, 1980).

Role of temperature

Two lines of thought suggest that the MD population is adapted to a narrower temperature range than the FT population. First, body size of the MD population

changes little over the temperature range examined in this study relative to that of the FT population. Body size may change little, or be directly related to temperature, outside an optimal temperature range, as reported for hemimetabolous aquatic insects (Sweeny and Vannote, 1978). Second, MD individuals occur in non-diapausing states over the temperature range of about 12–27°C, but the greater portion of their development and reproduction in the lake occurs between 20–26°C. In contrast, FT individuals may develop through all stages and reproduce in the lake over a temperature range of about 12–31°C, though reproduction nearly ceases between 12–15°C (Wyn-gaard *et al.*, 1982). *Mesocyclops* is subtropical in origin (Rylov, 1948) and 15°C probably represents a lower thermal boundary for development.

The near cessation of reproduction by the MD adult females at 15°C is a striking contrast to the fecund FT population. The MD females reared at 15°C certainly were not in diapause, as they actively swam and consumed live *Diatomus* prey as well as males of *M. edax* that were presented to them for mating purposes. Diapause in *M. edax* is usually characterized by arrested development at the fourth copepodid stage, accumulation of lipids, presence of mudcaps on either side of the cephalothorax, and a quiescent period during which the animals sink to the bottom muds during the fall and remain there until they emerge into the water column the following spring (Comita, 1972; Stucke, 1981). Diapause of adult females has also been reported in a Connecticut population (Elgmork, Univ. of Oslo, pers. comm.). It is possible that insemination occurred, but that 15°C was too cold for fertilization or production of egg sacs. Low temperatures prevent inseminated females of the marine copepod *Acartia tonsa* from producing egg sacs (Lonsdale, SUNY, Stony Brook, pers. comm.).

Genetic differentiation with regard to temperature has been suggested to be more prevalent in stenothermal species or races; acclimation, in eurythermal species or races (Precht *et al.*, 1973). Herzig's suggestion that the relative importance of genetic differentiation and acclimation may shift according to the temperature and geographic ranges experienced by the particular zooplankton species seems plausible in the context of the present study. He suggested that the more rapid development of *M. edax* eggs of an Ontario pond population (Carter, 1974) relative to a Lake Ontario population (Cooley, 1978) reflected adaptation to different temperature regimes. *M. edax* is a warm water copepod and Herzig's comparisons, as well as those in the present study, seem consistent with the view that genetic adaptation (or genetic differentiation) rather than acclimation is responsible for much of the phenotypic variation observed in field populations of *M. edax*. The ground water species *Speocyclops gallicus* is an extreme case of a copepod that experiences nearly constant temperature conditions, and shows a great degree of genetic adaptation in temperature related traits such as egg stage duration (Lescher-Moutoué, 1973). In contrast to the temperature responses of stenothermal copepods, the estuarine eurythermal copepod *Eurytemora affinis*, which typically experiences a temperature range of 0–30°C, shows considerable acclimation (Bradley, 1978a, b). The different measurement techniques used by different investigators may lead to a potential difficulty in distinguishing adaptation from acclimation in these studies. The environmental temperatures experienced by both populations in the present study, however, do not help explain why the FT individuals attained greater size or matured more rapidly than did MD individuals at an intermediate temperature (25°C).

Confounding selection pressures likely contribute to the complexity of these life histories and the difficulties of attributing the observed differences among populations to one factor or another. In addition to temperature, abundance of food and predators has been measured in the study lakes (cited below) and received considerable attention in the zooplankton literature as potential selective forces that influence life histories. Thus, it seems appropriate to comment on the possible relevance of differences in

food level and predator abundance among the study lakes to the genetic differentiation observed in this study.

Role of food level

The two northern sites did not differ greatly from one another in any obvious factors such as trophic status and, probably for that reason, exhibited no genetic differentiation except for one trait, female maturation time. The Florida locale afforded an opportunity to examine two lakes that are situated in close proximity but have grossly different trophic status (Wyngaard *et al.*, 1982; Dawes and Cowell, 1984; present study) and community structure (Elmore, 1983) in the same geographical region. For this reason, genetic differentiation may be greater between the two Florida populations. Elmore (1983) showed that the high and low food levels in Lake Thonotosassa and Fairy Lake, respectively, coupled with differences in predator abundance, constitute different selective regimes for three diptomid copepod species. Food and predation determined, in large part, their distribution and life history characteristics.

The small body size, slow maturation, small clutches, and large eggs of the Michigan populations may be viewed as consequences of selection to minimize energy demands when food is scarce. *In situ* culture of MD and FT individuals in (low-food) Douglas Lake revealed that MD individuals hatched from larger eggs into larger nauplii and exhibited higher survival to maturity than did FT individuals (Wyngaard, unpub. ms.). Allan (1984) found this difference in egg size to be genetic and reported a negative phenotypic correlation between egg size and clutch size when the MD and FT populations were pooled, suggesting a tradeoff between the traits of egg size and clutch size.

Role of predation

Lake Thonotosassa contains high densities of planktivorous fishes, the most abundant of which is gizzard shad (Langford, 1975). Fairy Lake contains no shad. FT individuals undergo a pronounced diel vertical migration (Wyngaard, 1978) whereas the FF individuals do not do so. This is consistent with the view that vertical migration behavior is a response to the feeding behavior of fish (Zaret and Suffern, 1976). It has been argued that predation selects for rapid maturation (Charlesworth, 1980) and small size at first reproduction (Brooks and Dodson, 1965). The rapid maturation of FT individuals may be a response to such predation pressure. The large body sizes of the FT individuals may seem inconsistent with this view, but gizzard shad in Lake Thonotosassa likely feed upon zooplankton using a pump filter mechanism rather than visual attack on plankton (Drenner *et al.*, 1982).

While the Michigan lakes contain planktivorous fishes (Fairchild, 1980; Smith, American Museum of Natural History, unpub. data) the higher densities of shad in Lake Thonotosassa probably represent a level of predation much greater than that of Lake Cochran or Douglas Lake. Fairy Lake and the two Michigan lakes contain high densities of daphnids (Young, 1978; Fairchild, 1980; Dawes and Cowell, 1984; Gannon, SUNY at Oswego, unpub. data), which are not typically abundant in lakes with high densities of planktivorous fish. The low food levels in these three lakes may exhibit more influence on life history characteristics than predation, resulting in small body sizes and slow maturation. The interplay among temperature, predation, and resource availability is difficult to dissect. The present study hints at what might be the relative importance to life histories of these factors in specific populations.

These interpretations of genetic differentiation among the four *M. edax* populations represent hypotheses describing how different environments may have selected for different life histories. Perhaps what is most intriguing is the observation of two seem-

ingly distinct life history tactics: (1) rapid maturation, large body, large clutches, and small eggs in the Florida population and (2) slow maturation, small body, small clutches, and large eggs in the Michigan population. It would be of interest to investigate whether these assemblages of traits represent tightly, co-adapted complexes of life history traits, or alternatively, independently evolving individual traits.

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LITERATURE CITED

- ALLAN, J. D. 1984. Life history variation in a freshwater copepod: evidence from population crosses. *Evolution* **38**: 280-291.
- ANTONOVICS, J., AND A. D. BRADSHAW. 1970. Evolution in closely adjacent plant populations. VIII. Clinal patterns in *Anthoxanthum odoratum* across a mine boundary. *Heredity* **25**: 349-362.
- BATTAGLIA, B. 1959. Il polimorfismo adattativo e i fattori della selezione nel copepoda *Tisbe reticulata* Bocquet. *Arch. Oceanogr. Limnol.* **11**: 19-69.
- BEAVER, J. R., AND T. L. CRISMAN. 1982. The trophic response of ciliated protozoans in freshwater lakes. *Limnol. Oceanogr.* **27**: 246-253.
- BERVEN, K. A. 1982a. The genetic basis of altitudinal variation in the wood frog, *Rana sylvatica*. I. An experimental analysis of larval development. *Oecologia* **52**: 360-369.
- BERVEN, K. A. 1982b. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*. II. An experimental analysis of life history traits. *Evolution* **36**: 962-983.
- BRADLEY, B. P. 1978a. Genetic and physiological adaptation of the copepod *Eurytemora affinis* to seasonal temperatures. *Genetics* **90**: 193-205.
- BRADLEY, B. P. 1978b. Increase in range of temperature tolerance of acclimation in the copepod *Eurytemora affinis*. *Biol. Bull.* **154**: 177-187.
- BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. *Science* **150**: 28-35.
- BRUGIS, M. J. 1970. The effect of temperature on the development time of eggs of *Thermocyclops* sp., a tropical cyclopoid copepod from Lake George, Uganda. *Limnol. Oceanogr.* **15**: 742-747.
- CARLSON, R. E. 1977. A trophic state index for lakes. *Limnol. Oceanogr.* **22**: 361-368.
- CARTER, J. C. H. 1974. Life cycles of three limnetic copepods in a beaver pond. *J. Fish. Res. Board Can.* **31**: 421-434.
- CHARLESWORTH, B. 1980. *Evolution in Age-structured Populations*. Cambridge Studies in Mathematical Biology. Cambridge University Press, Cambridge. 300 pp.
- CLAUSEN, J., D. D. KECK, AND W. M. HIESEY. 1948. Experimental studies on the nature of species. III. Environmental responses of the climatic races of *Achillea*. Carnegie Institution of Washington, Publ. No. 581, 129 pp.
- COKER, R. E. 1933. Influence of temperature on size of freshwater copepods (*Cyclops*). *Internationale Revue der Gesamten Hydrobiologie* **24**: 406-436.
- COKER, R. E. 1943. *Mesocyclops edax* (S. A. Forbes), *M. leuckarti* (Claus) related specimens in America. *Elisha Mitchell Sci. Soc.* **59**: 181-200.

- COMITA, G. 1972. The seasonal zooplankton cycles, production and transformation of energy in Severson Lake, Minnesota. *Arch. Hydrobiol.* **70**: 14-66.
- GOODRICH, M. 1978. The effect of temperature and the development of diapausing and subitaneous eggs in several freshwater copepods. *Crustaceana* **35**: 27-34.
- COMPTON, B. C., C. W. DYE, AND R. C. ADAMS. 1975. A synoptic study of the limnology of Lake Thonotosassa, Florida. Part I. Effects of primary treated sewage and citrus wastes. *Hydrobiologia* **46**: 301-345.
- DAWES, C., AND B. C. COWELL. 1984. Algal studies of eutrophic Florida lakes: determination of factors responsible for nuisance blooms of planktonic algae in central Florida. Final Report. Florida Dept. of Natural Resources. 133 pp.
- DINGLE, H., AND J. P. HEGMANN, eds. 1982. *Evolution and Genetics of Life Histories*. Springer Verlag, New York. 250 pp.
- DRENNER, R. W., F. DEHOYELLES, JR., AND D. KETTLE. 1982. Selective impact of filter-feeding gizzard shad on zooplankton community structure. *Limnol. Oceanogr.* **27**: 965-968.
- ELMORE, J. L. 1980. An experimental study of factors regulating the distribution of *Diaptomus* (Copepoda: Calanoida) in subtropical Florida. Ph.D. Thesis, University of South Florida, Tampa, Florida.
- ELMORE, J. L. 1983. Factors influencing *Diaptomus* distributions: an experimental study in subtropical Florida. *Limnol. Oceanogr.* **29**: 522-532.
- ENDLER, J. A. 1973. Gene flow and population differentiation. *Science* **179**: 243-250.
- FAIRCHILD, G. W. 1980. Effects of littoral conditions on the distribution, behavior, and population dynamics of a filter feeding microcrustacean: *Sida crystallina*. Dissertation. University of Michigan, Ann Arbor, Michigan.
- FORBES, E. B. 1897. A contribution to a knowledge of North American fresh-water Cyclopidae. *Bull. Ill. State Lab.* **5**: 27-83.
- GANNON, J. E., AND M. W. PADDOCK. 1974. *Investigation into Ecological and Sociological Determinants of Land-use decisions—A Study of Inland Lake Watersheds in Northern Michigan*. University of Michigan Biological. Station Technical Report No. 1.
- HALL, D. J. 1964. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. *Ecology* **45**: 94-117.
- HELWIG, J. T., AND K. A. COUNCIL, eds. 1979. SAS User's Guide, 1979 editions. SAS Institute Inc., Cary, NC.
- HERZIG, A. 1983. The ecological significance of the relationship between temperature and duration of embryonic development in planktonic copepods. *Hydrobiologia*. **100**: 65-91.
- JAIN, S. K., AND A. D. BRADSHAW. 1966. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. *Heredity* **21**: 407-441.
- KERFOOT, W. C., ed. 1980. *Evolution and Ecology of Zooplankton Communities*. Univ. Press New England, Hanover, N. H. 793 pp.
- LANDE, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* **63**: 607-615.
- LANGFORD, F. 1975. *Lake Thonotosassa Status Report*. March. State of Florida Game and Freshwater Fish Commission. 8 pp.
- LESCHER-MOUTOUE, F. 1973. Sur la biologie et l'ecologie des Copepodes Cyclopidés hypogés (Crustacés). *Ann. Spéol.* **28**: 429-502, 581-674.
- LIND, O. T. 1978. Interdepression differences in the hypolimnetic areal relative to oxygen deficits of Douglas Lake, Michigan. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **10**: 528-538.
- MCLAREN, I. A. 1965. Some relationships between temperature and egg size, body size, development rate and fecundity of the copepod *Pseudocalanus*. *Limnol. Oceanogr.* **10**: 528-538.
- MCLAREN, I. A. 1976. Inheritance of demographic and production parameters in the marine copepod *Eurytemora herdmanni*. *Biol. Bull.* **151**: 200-213.
- MCNEILLY, T. 1968. Evolution in closely adjacent plant populations. III. *Agrostis tenuis* in a small copper mine. *Heredity* **23**: 99-108.
- PRECHT, H., J. CHRISTOPHERSON, H. HENSEL, AND W. LARCHER. 1973. *Temperature and Life*. Springer Verlag, Berlin. 779 pp.
- RYLOV, V. M. 1948. *Freshwater Cyclopoida-Fauna of U.S.S.R. Crustacea*. Vol. 3, No. 3 Israel Program for Scientific Translations, Jerusalem.
- SOKAL, R. R., AND F. J. ROHLF. 1969. *Biometry*. W. H. Freeman and Company, San Francisco. 776 pp.
- STUCKE, D. E. 1981. Seasonality and distribution of two limnetic copepods, *Diacyclops bicuspidatus thomasi* S. A. Forbes 1882 and *Mesocyclops edax* (S. A. Forbes) 1881, in relation to lake thermal and oxygen structure. M. S. Thesis, Case Western University. 148 pp.
- SWEENEY, B. W., AND R. L. VANNOTE. 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science* **200**: 444-446.
- TUCKER, A. 1957. The relation of phytoplankton periodicity to the nature of the physicochemical environment with special reference to phosphorus. Morphometrical, physical and chemical conditions. *Am. Midl. Nat.* **57**: 300-370.

WELCH, P. S. 1927. Limnological investigations in northern Michigan lakes. I. Physical-chemical studies on Douglas Lake. *Pap. Mich. Acad. Sci. Arts and Lett.* **8**: 421-451.

WILSON, M. S., AND H. C. YEATMAN. 1959. Free-living Copepoda. In *Freshwater Biology*, Second ed. H. B. Ward and G. C. Whipple, eds. John Wiley & Sons Inc.

WYNGAARD, G. A. 1978. The relationship between the reproductive rate of a predaceous copepod, prey item abundance and temperature. M. S. Thesis, University of South Florida. Tampa. 57 pp.

WYNGAARD, G. A. 1986. Heritable life history variation in widely separated populations of *Mesocyclops edax* (Copepoda). *Biol. Bull.* **170**: 296-304.

WYNGAARD, G. A. 1983a. *In situ* life table of a subtropical copepod. *Freshwater Biol.* **13**: 275-281.

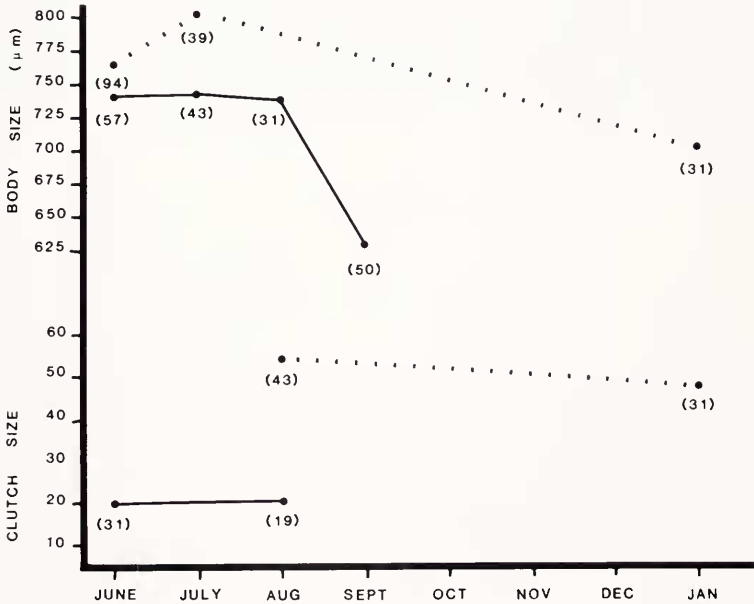
WYNGAARD, G. A. 1983b. An experimental analysis of the genetic basis of life history variation in *Mesocyclops edax* (Crustacea: Copepoda). Ph.D. Diss., University of Maryland. 94 pp.

WYNGAARD, G. A., AND C. C. CHINNAPPA. 1982. Biology and cytology of cyclopoids. Pp 485-553 in *Developmental Biology of Freshwater Invertebrates*, F. W. Harrison and R. R. Cowden, eds. Alan R. Liss, New York.

WYNGAARD, G. A., J. L. ELMORE, AND B. C. COWELL. 1982. Dynamics of a subtropical plankton community, with emphasis on the copepod *Mesocyclops edax*. *Hydrobiologia* **89**: 36-48.

YOUNG, S. N. 1978. Relationship between abundance of crustacean zooplankton and trophic state in fourteen central Florida lakes. Masters Thesis, University of South Florida. Tampa, Florida.

ZARET, T. M., AND J. S. SUFFERN. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* **21**: 804-813.



APPENDIX. Body size (µm) and clutch size of *Mesocyclops edax* collected from Douglas Lake, Michigan (—) and Lake Thonotosassa, Florida (---). Numbers in parentheses refer to numbers of individuals.